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Reproductive biology of the sea anemone shrimp *Periclimenes rathbunae* (Caridea, Palaemonidae, Pontoniinae), from the Caribbean coast of Costa Rica

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Abstract

Caridean shrimps are a highly diverse group and many species form symbiotic relationships with different marine invertebrates. *Periclimenes rathbunae* is a brightly colored shrimp that lives predominantly in association with sea anemones. Information about the reproductive ecology of the species is scarce. Therefore, we collected 70 ovigerous females inhabiting the sun sea anemone *Stichodactyla helianthus* in coral reefs from the southern Caribbean coast of Costa Rica. Females produced on average 289 ± 120 embryos. The volume of recently-produced embryos was on average 0.038 mm^3, and embryo volume increased by 192% during the incubation period. The average embryo mortality during embryogenesis was 24%. The reproductive output was 0.24 ± 0.094, considerably higher than in many other pontoniine shrimps. Females carrying embryos close to hatching showed fully developed ovaries, suggesting consecutive spawning. We assume that the sheltered habitat, living on sea anemones, allows *P. rathbunae* to allocate more energy in embryo production than most other free-living caridean shrimps. This is the first record of *P. rathbunae* for Costa Rica.

Keywords

Coral reefs, fecundity, new record, reproductive output, symbioses

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Introduction

Caridean shrimps are a highly diverse group within the Decapoda, comprising approximately 3438 currently valid species within 389 genera (De Grave and Fransen 2011). They inhabit a wide range of habitats (Chace 1972, Bauer 1985, Anker 2003, De Grave et al. 2008), and have different niches (Welsh 1975, Bauer 2004, Hultgren and Duffy 2012), mating behaviors (Berg and Sandifer 1984, Thiel and Hinojosa 2003, Bauer and Thiel 2011, Baeza et al. 2013), and reproductive features (Gherardi and Calloni 1993, Bauer 2000, Echeverría-Sáenz and Wehrtmann 2011, Nye et al. 2013). Caridean shrimps have been relatively well studied, mainly due to the fact that many species are valuable fishery resources (Clarke et al. 1991). Other shrimps have been targeted by the aquarium trade as ornamental species, due to their bright colors and display of associative behavior with other marine species (Calado et al. 2003a, Rhyne et al. 2009).

Many studies report on symbiotic relationships between caridean shrimps and other invertebrates, such as sponges, cnidarians, echinoderms, mollusks, crustaceans, and also with fishes (Bruce 1976, Criales and Corredor 1977, Bauer 2004). The symbiotic partner can receive cleaning services (Limbaugh et al. 1961, Criales and Corredor 1977), protection from predators (Smith 1977), burrow access (Karplus 1987), or increased nitrogen concentrations from shrimp excretions (Spotte 1996). On the other hand, caridean symbionts often benefit by protection from predators or feeding on the host tissue (Fautin et al. 1995, Silbiger and Childress 2008), and increased chances for successful reproduction (Kotb and Hartnoll 2002).

The highly diverse genus *Periclimenes* Costa, 1844 comprises approximately 152 species (De Grave and Fransen 2011). Many species of *Periclimenes* are usually associated with different marine invertebrates such as sea anemones, corals, sea stars and sea cucumbers (Bruce 2004). *Periclimenes rathbunae* Schmitt, 1924 is a brightly colored shrimp recorded from Florida (USA), Mexico, Belize, Colombia, Cuba, Turks and Caicos, Tobago, and Curaçao (Chace 1972, Román-Contreras and Martínez-Mayén 2010). The species has been found associated to a variety of different shallow-water sea anemones such as *Bartholomea annulata* (Le Sueur, 1817), *Bunodosoma granuliferum* (Le Sueur, 1817), *Condylactis gigantea* (Weinland, 1860), *Homostichanthus duerdeni* (Carlgren, 1900), *Lebrunia neglecta* Duchassaing & Michelotti, 1860 and *Stichodactyla helianthus* (Ellis, 1768) (Spotte et al. 1991, Hayes and Trimm 2008). However, it has been also collected from the gorgonian *Eunicea tourneforti* Milne Edwards & Haime, 1857 (see Criales 1980) and from dead corals (Chace 1972). Biological studies on *P. rathbunae* have focused mainly on their ecology and hosts (Spotte et al. 1991, Hayes and Trimm 2008) but information about reproductive features is scarce (Spotte 1997).

Hines (1982, 1988, 1991) studied the reproductive output (RO) of different marine decapods and reported RO values around 10% for a variety of brachyuran crab species. However, decapod species living as commensals (e.g. in bivalves and corals) and with a reduced calcification of the integument can allocate substantially more energy in embryo production (e.g. pea crabs *Zaops ostreus* (Say, 1817) and *Fabia subquadrata* Dana, 1851: Hines 1992; coral gall crab *Hapalocarcinus marsupialis* Stimpson, 1859:

Kotb and Hartnoll 2002). Here we studied fecundity and reproductive output of *P. rathbunae* in order to test the hypothesis that pontoniine shrimps living as symbionts with other invertebrates can invest more energy in embryo production that free-living shrimps but less than decapods living enclosed in other invertebrates.

Methods

Ovigerous females of *P. rathbunae* were collected during five field trips (September and October 2011, January, June and October 2012) in the Puerto Viejo-Punta Mona coral reef area (Cortés et al. 2010) within the Gandoca-Manzanillo National Wild Life Refuge, at the southern Caribbean coast of Costa Rica (Fig. 1). The sea surface temperature in all sampling months varied between 27 and 30 °C (data provided by MIO-CIMAR: http://www.miocimar.ucr.ac.cr/). The substrate was dominated by algal ridges, with low live coral cover, ranging from 8 to 16%, although this percentage has been increasing during the last decades (Cortés et al. 2010). All specimens were collected between 1-4 m depth, and were associated with the sun sea anemone, *S. helianthus* Ellis, 1768. The shrimps were collected by hand during snorkeling dives and placed individually into plastic vials. The collected specimens were stored and preserved in 70% ethanol, and subsequently transported to the laboratory at the Escuela de Biología, Universidad de Costa Rica, in San José. The shrimps were identified according to Chace (1972) and photos provided by Dr Arthur Anker. Six specimens were deposited in the Museo de Zoología of the Universidad de Costa Rica (catalog number MZUCR 3155-01). The material was collected under the sampling permit No. 181-2013 provided by SINAC-MINAET.

The total length (TL, distance between distal part of the eye socket to the distal margin of the telson excluding setae) and carapace length (CL, distance between distal part of the eye socket to the posterior margin of the carapace) were measured with the aid of Leica MS5 stereoscopic microscope equipped with a calibrated ocular micrometer. Linear regression was performed to test the relationship between TL and CL. The entire embryo mass was removed from females and photographed to count the number of embryos, using IMAGE TOOL version 3.00 developed by UTHSCSA. Here we used the term fecundity as the number of embryos carried by the female (Corey and Reid 1991). The female length and the number of embryos were correlated using linear regression analysis. Thirty embryos of each clutch were separated, and length and width of embryos were measured under a Leica CME microscope equipped with a calibrated ocular micrometer. The embryo volume was calculated using the formula for oblate spheroids $V = 1/6 (\pi d_1 \times d_2^2)$ where d_1 is the mayor diameter, and d_2 is the perpendicular diameter (Turner and Lawrence 1979). The brood mass volume was estimated multiplying total embryo number per female by their respective average embryo volume (Echeverría-Sáenz and Wehrtmann 2011).

The stage of embryo development was assigned following the criteria described by Wehrtmann (1990): Stage I, uniform yolk, no eye pigments observed; Stage II, eye pigments start to develop; Stage III, embryo clearly visible and fully developed. The

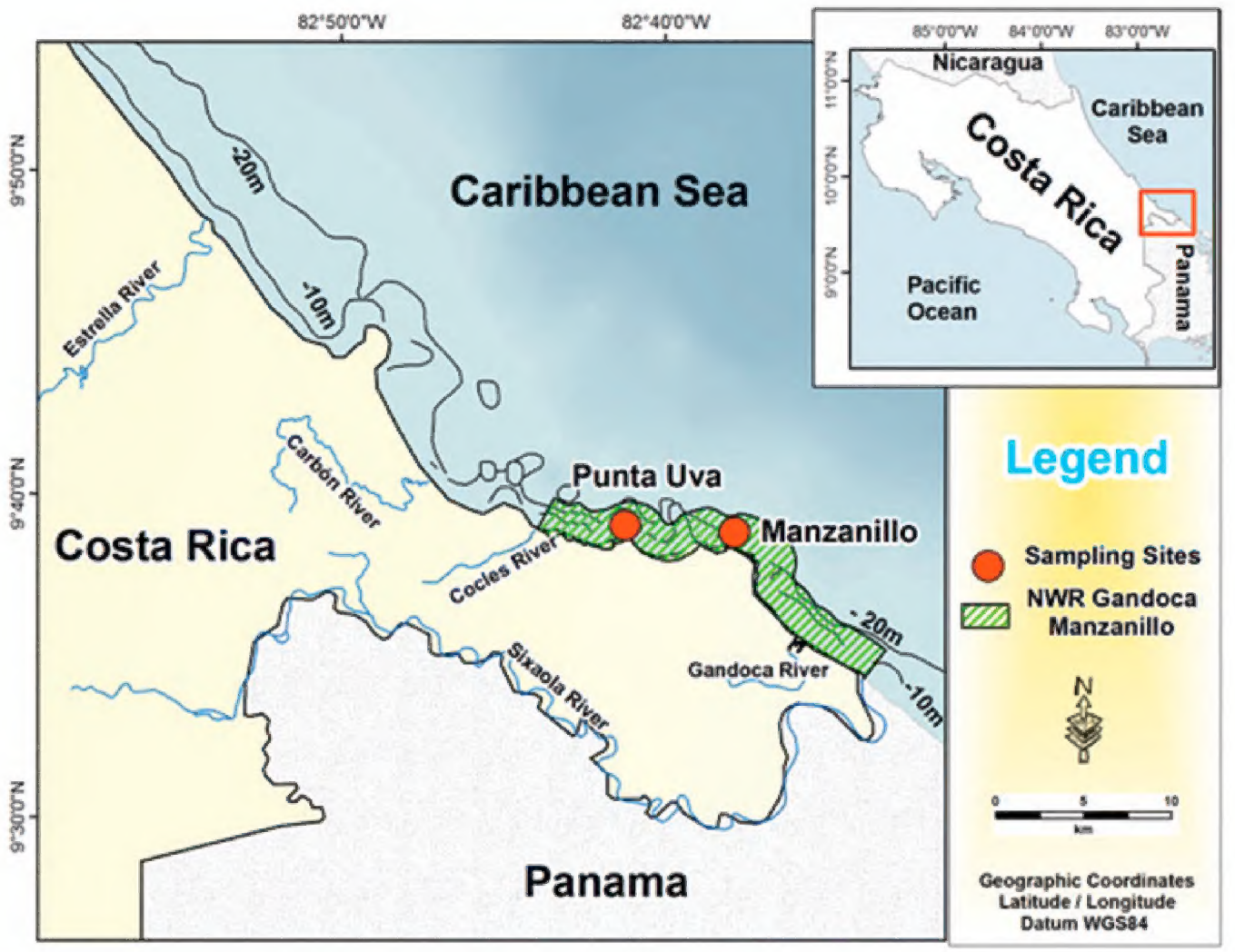

Figure 1. Sampling sites of *Periclimenes rathbunae* visited between 2011 and 2012: Punta Uva and Manzanillo beaches, Gandoca-Manzanillo National Wild-Life Refuge, Caribbean coast of Costa Rica.

number of embryos, embryo volume and brood mass volume were compared between developmental stages of the embryos using one-way analysis of variance. Females and brood masses were dried separately at 60 °C for 48 hours, and the dry weight was measured using a Sartorius TE64 analytical balance (± 0.0001) to calculate the reproductive output (RO): dry weight of total brood mass per female divided by dry weight of female without brood mass (Hines 1988, Echeverría-Sáenz and Wehrtmann 2011). The RO was estimated exclusively for females carrying recently-extruded embryos (Stage I).

The stage of ovarian development was determined following the criteria proposed by Bauer (1986): Stage 1, no noticeable development; Stage 2, vitellogenic oocytes distinct but small ovary; Stage 3, ovary filling at least half the space above the cardiac stomach; Stage 4, ovary completely filling the space above the cardiac stomach. The ovarian and embryos development were analyzed to infer the possibility of consecutive spawning (Bauer 1986, 1992).

Results

A total of 70 ovigerous females of *P. rathbunae* were analyzed; TL of these specimens was directly proportional to CL (CL = 0.1657 × TL + 0.5497; F = 313.21; DF = 69;

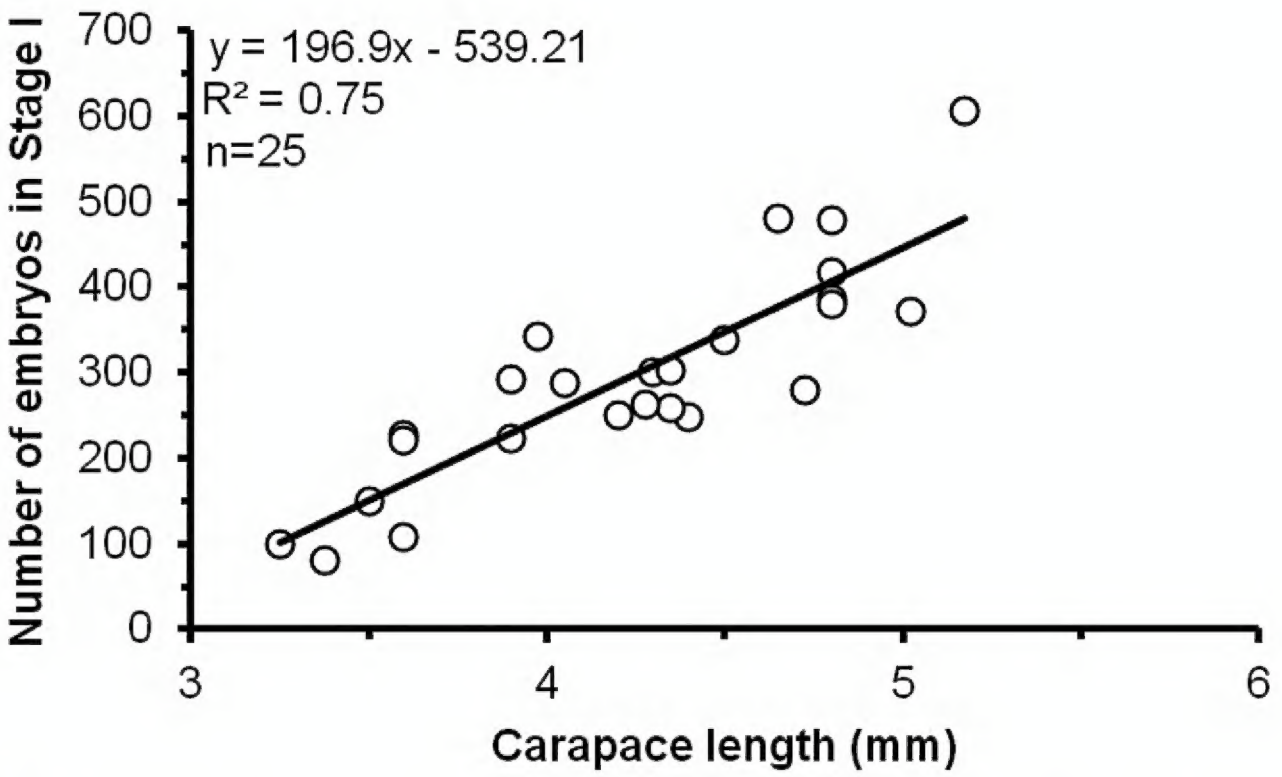

Figure 2. Relation between number of embryos in Stage I and female size of *Periclimenes rathbunae* from the Caribbean coast of Costa Rica, 2011–2012.

$P < 0.001$; $R^2 = 0.80$). Individuals ranged in size from 2.25 to 5.25 mm CL with an average of 3.98 ± 0.77 mm CL. A total of 29 females carried embryos in Stage I, 14 in Stage II, and 27 in Stage III.

Embryo number

The average number of Stage I embryos was 289 ± 120 embryos per female, with a minimum and maximum of 80 and 605, respectively. The number of recently-extruded embryos (Stage I) increased significantly with female size ($F = 69.1$; $DF = 23$; $P < 0.001$; $R^2 = 0.75$) (Fig. 2). The embryo number was significantly different between Stage I and III ($F = 3.5$; $DF = 66$; $P = 0.03$) (Table 1), but this difference was due to a significant decrease of embryo numbers from Stage II to Stage III ($F = 4.7$; $DF = 39$; $P = 0.03$). Average embryo number decreased during the incubation period by 24%.

Embryo volume and brood mass volume

Recently-produced embryos (Stage I) had an average volume of 0.038 mm^3, and those closed to hatching (Stage III) 0.073 mm^3 (Table 1), representing a volume increase of 192% during the incubation period. The average embryo volume ($F = 30.9$; $DF = 67$; $P < 0.001$) as well the average brood mass volume ($F = 4.5$; $DF = 66$; $P = 0.01$) was statistically different among the three developmental stages (Table 1). Average brood mass volume increased during embryogenesis from 10.6 to 15.1 mm^3 (Table 1), which represented a 42% increase.

Table 1. Number of analyzed specimens, mean ± standard deviation of carapace length (CL), embryo number, embryo volume, and brood mass volume according to the stage of embryo development in females of *Periclimenes rathbunae* from the Caribbean coast of Costa Rica, 2011–2012.

Stage of embryo development	n	CL (mm)	Embryo number	Embryo volume (mm^3)	Brood mass volume (mm^3)
I	29	4.2 ± 0.6	289 ± 120	0.038 ± 0.011	10.6 ± 4.6
II	14	4.3 ± 0.5	288 ± 105	0.050 ± 0.013	15.0 ± 6.8
III	27	4.2 ± 0.5	219 ± 90	0.072 ± 0.022	15.1 ± 6.7

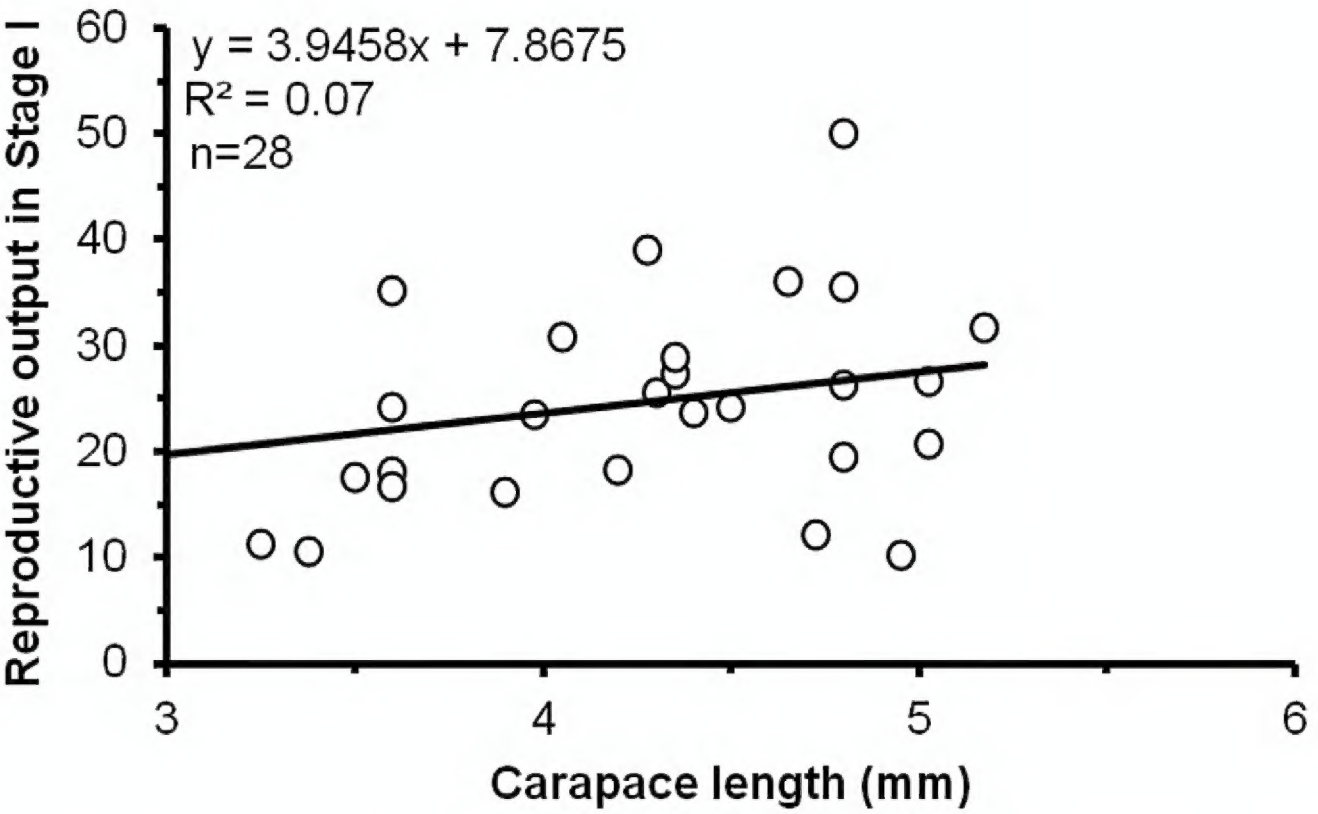

Figure 3. *Periclimenes rathbunae* from the Caribbean coast of Costa Rica, 2011–2012: relation between reproductive output (Stage I) and female size.

Reproductive output

The average RO for female *P. rathbunae* was 0.24 ± 0.094, fluctuating between 0.10 and 0.50. There was no significant correlation between RO and CL of females ($F = 2.0$; $DF = 26$; $P > 0.05$; $R^2 = 0.07$) (Fig. 3).

Reproductive activity

Ovigerous females were collected during all five field trips carried out between September 2011 and October 2012. Early ovarian stages (Stage 1–2) predominated in females carrying recently-extruded embryos (Stage I), while ovaries filled with vitellogenic oocytes (Stage 4) reached its highest occurrence in females with embryos close to hatching (Stage III) (Fig. 4).

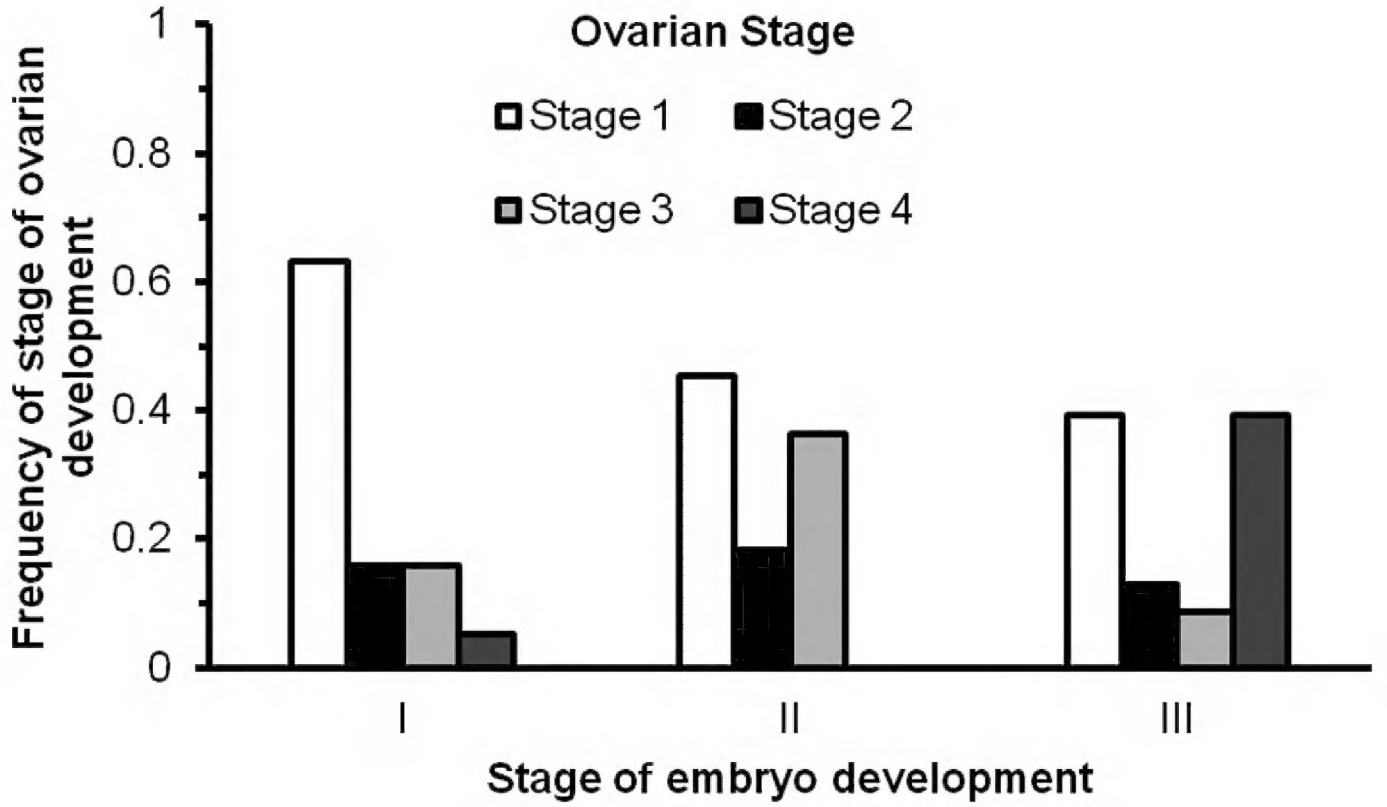

Figure 4. Frequency of stage of ovarian development in relation to the stage of embryo development from females of *Periclimenes rathbunae* from the Caribbean coast of Costa Rica, 2011–2012.

Discussion

This is the first record of *P. rathbunae* for Costa Rica. Vargas and Wehrtmann (2009) summarized the available information on marine decapod diversity in Costa Rica, but did not mention *P. rathbunae*; however, they pointed out that the Caribbean coast of Costa Rica was less studied than the Pacific coast of the country. This new record confirms the geographic distribution of the species, ranging from Florida (USA) to Curaçao (Chace 1972, Román-Contreras and Martínez-Mayén 2010).

Embryo number

The sea anemone shrimp *P. rathbunae* produces a relatively high number of offspring when compared to other pontoniine species (Table 2): only *Periclimenes ornatus* Bruce, 1969 has been reported to carry more embryos (Omori et al. 1994), but this species reaches also slightly larger sizes. Many studies on caridean shrimps revealed that fecundity is closely related to female size (for tropical palaemonids: Anger and Moreira 1998, Wehrtmann and Lardies 1999, Nazari et al. 2003, da Silva et al. 2004, Lara and Wehrtmann 2009, Meireles et al. 2013), and our data for *P. rathbunae* confirm this tendency (Fig. 2). We observed also sexual dimorphism in *P. rathbunae* with females reaching larger sizes than males (JC Azofeifa-Solano et al., unpubl data), a phenomenon well-known in many caridean shrimps (Bauer 2004), and also reported for *P. ornatus* by Omori et al. (1994) who found that males attained smaller sizes, but had larger chelae than females.

Table 2. Minimum and maximum female carapace length (CL), embryo number in Stage I, mean embryo volume and reproductive output (RO) in Stage I, habitat and study site of seven pontoniine species; NA = no data available; * = total length. ** = Value recalculated by the authors of the present study (see Discussion).

Species	CL (mm)	Embryo number	Embryo volume (mm^3)	RO (%)	Habitat	Study site	Reference
Periclimenes ornatus Bruce, 1969	3.0–6.0	10–1000	0.49 (0.06**)	NA	Sea anemone	Shikoku Island, Japan	Omori et al. (1994)
Ancylomenes pedersoni (Chace, 1958) Reported as *Periclimenes anthophilus*	NA	33–80	0.05	NA	Sea anemone	Bermuda	Spotte (1999)
Ancylomenes pedersoni (Chace, 1958) Reported as *Periclimenes pedersoni*	NA	78–221	0.11	NA	Sea anemone	Bahamas	Spotte (1999)
Periclimenes pandionis Holthuis, 1951	2.84–4.0	67–259	0.05	NA	Coral reef	Indian River, Florida	Corey and Reid (1991)
Periclimenes patae Heard & Spotte, 1991	3.3–4.2	10–35	NA	NA	Gorgonian	Turks and Caicos and Florida Keys	Heard and Spotte (1991)
Periclimenes yucatanicus (Ives, 1891)	3.52–5.73	12–333	NA	NA	Sea anemone	West Indies and south Florida	Spotte (1997)
Phycomenes siankaanensis (Martinez-Mayén & Román-Contreras, 2006)	1.91–3.2	23–141	0.056	NA	Sea grass meadow	Quintana Roo, Yucatan Peninsula, Mexico	Martínez-Mayén and Román-Contreras (2009)
Periclimenes rathbunae Schmitt, 1924	2.25–5.25 (12.3–22.6*)	80–605	0.038	24.0 ± 0.09	Sea anemone	Limón, Costa Rica	Present study

Embryo volume and brood mass volume

The average embryo volume of *P. rathbunae* is in the range of most values reported for other pontoniine species (Table 2). However, *P. ornatus* in southwest Japan produces considerably larger embryos with a maximum volume of 0.49 mm^3 (Omori et al. 1994). However, these authors did not explain how they calculated the embryo volume. Using the average values for embryo length and width provided by Omori et al. (1994), and applying the same equation as used in the present study (Turner and Lawrence 1979), average embryo volume of *P. ornatus* would be 0.06 mm^3, which is in the range reported for other pontoniine species, including *P. rathbunae* (Table 2). Both species, *P. rathbunae* and *P. ornatus*, share similar size ranges and live associated with sea anemones in tropical and subtropical waters (Chace 1972, Omori et al. 1994). Most species of pontoniine shrimps producing these relatively small embryos, including *P. rathbunae*, probably have an extended larval development. There is still a great lack of knowledge concerning the complete larval development of most of the pontoniine species; however, dos Santos et al. (2004) cultivated *Periclimenes sagittifer*

Norman, 1861 in the laboratory and described eight zoeal stages, corroborating an extended larval period.

Periclimenes rathbunae lost during the incubation period on average 24% of the initially-produced embryos, while embryo volume increased by 192%. Brood loss in *P. rathbunae* was similar to that reported for other palaemonid freshwater shrimps: approximately 23% in *Palaemon pandaliformis* (Stimpson, 1871) and *Macrobrachium acanthurus* (Wiegmann, 1836) (Kuris 1991, Anger and Moreira 1998) and was slightly higher than the 17.2% of brood loss observed in the marine palaemonid *Palaemon gravieri* (Yu, 1930) (see Kim and Hong 2004). Furthermore, it was higher than the brood loss reported for the sponge-dwelling snapping shrimp *Synalpheus yano* (Ríos & Duffy, 2007) from Panama (Hernáez et al. 2010). The volume increase of caridean shrimp embryos during the incubation period ranges from 3.9 to 155.9% (Corey and Reid 1991); thus the observed value for *P. rathbunae* is considerably higher than this range. The combination of relatively low brood loss and substantial embryo volume increase during embryogenesis in *P. rathbunae* suggests that the physical space available for embryo attachment is sufficient to accommodate and maintain the clutch until hatching. The association with the sea anemone and efficient parental care during the incubation period may provide favorable conditions for the embryo development, and thus reducing brood loss during the embryogenesis. Such an interpretation is in agreement with similar observations in *S. yano*, a pair-living and sponge-dwelling alpheid species from tropical waters (Hernáez et al. 2010).

Reproductive output

The RO is a widely used instrument to document and compare inter- and intra-specifically energy allocation in offspring production of decapod crustaceans (Clarke et al. 1991, Hines 1991, Lardies and Wehrtmann 1996, Anger and Moreira 1998, Terossi et al. 2010, Echeverría-Sáenz and Wehrtmann 2011). To our best knowledge, here we report the first RO value for any pontoniine species (Table 2). The RO of *P. rathbunae* females (0.24) was higher than that reported for some free-living marine shrimps: 14.4 ± 2.5% for *Palaemon northropi* (Rankin, 1898) (see Anger and Moreira 1998) and 17.8 ± 6.0% for *Heterocarpus vicarius* Faxon, 1893 (see Echeverría-Sáenz and Wehrtmann 2011); and freshwater shrimps: 18.6 ± 3.0% for *P. pandaliformis* (Stimpson, 1871) (see Anger and Moreira 1998), 19.1 ± 4.5% for *M. acanthurus* (Wiegmann, 1836) (see Anger and Moreira 1998), 21.7 ± 6.6% for *Macrobrachium olfersii* (Wiegmann, 1836) (see Anger and Moreira 1998), and 3.6 ± 1.9% for *Atya scabra* (Leach, 1816) (see Herrera-Correal et al. 2013). These results suggest that marine caridean shrimps species living in association with other invertebrates are able to invest on average more energy in brood production than free-living species. Nevertheless, we suggest analyzing the RO within the subfamily Pontoniinae between free living and symbiont species in order to test if a sheltered habitat is related to an increase in RO in this diverse group of shrimps.

The reduction of the calcification of the exoskeleton results in a minimized dry weight of the decapod species, thus increasing its relative brood weight (Hines 1992; Kotb and Hartnoll 2002). The symbiont *H. marsupialis*, a species which provokes gall development in its host coral has a reproductive investment per brood of 59% (Kotb and Hartnoll 2002), and this value is still lower than those published for symbiotic decapods, such as the pea crabs *Z. ostreus* (66%) and *F. subquadrata* (97%) (Hines 1992). While the coral gall crab and the pea crabs live protected within galls of corals and bivalves, respectively, species like *P. rathbunae* are associates on other invertebrates, more exposed to predation and wave action than the above-mentioned crab species. This may explain the relatively high RO value in *P. rathbunae* compared to free-living decapods, but substantially lower RO-value when compared to symbiotic decapods living enclosed within their host. Additional studies with decapod species living in association with other invertebrates are needed to substantiate the hypothesis of increasing energy allocation in brood production with increasing degree of protection provided by the host.

Reproductive activity

Relatively elevated and stable temperatures in tropical seas may allow year-round reproduction of marine decapods (Bauer 1986, 1992). Our results concerning the relation between the state of ovarian development and stage of embryo development as well as the fact that ovigerous females of *P. rathbunae* were encountered throughout the sampling period confirms that this species has continuous reproduction (Mossolin and Bueno 2002). Bauer (1992) studied reproductive patterns in different caridean shrimps, including *Cuapetes americanus* (Kingsley, 1878) associated with sea grass meadows in Puerto Rico; his results revealed that all of these caridean species go through continuous cycles of ovarian maturity and spawning until they die. Our results corroborate the generalized pattern of continuous reproduction in tropical shallow-water shrimps and confirm *P. rathbunae* as an iteroparous species.

In recent years, the pressure on ornamental species has increased, and this includes also decapod species, which are highly popular among aquarium hobbyists (Calado et al. 2003a). As far as we know, *P. rathbunae* has not been harvested yet at the Caribbean coast of Costa Rica; however, its eye-catching color pattern and the fact that the shrimp lives in association with sea anemones makes it a potential candidate for aquarium hobbyists, just as numerous other pontoniine species (see Calado et al. 2003a). In order to minimize possible negative impacts caused by the harvest of wild marine species such as *P. rathbunae* (see Wood 2001), additional information on larval development is needed to cultivate the early life stages under controlled laboratory conditions (Calado et al. 2003b). Moreover, many other aspects of the ecology of *P. rathbunae* remain to be studied, e.g., mating behavior, recruitment, settlement on the host species as well as other details about the association of the shrimp with its host.

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